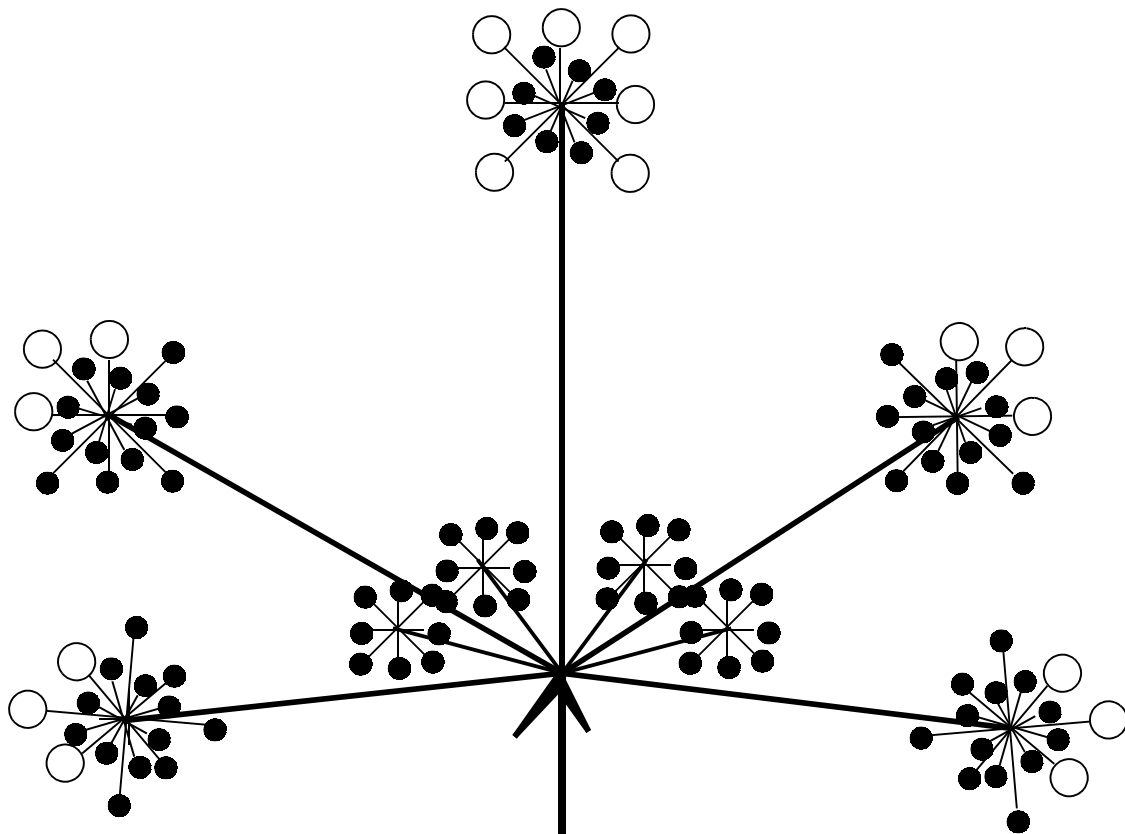

POPULATION BIOLOGY OF *LOMATIUM BRADSHAWII*

II. INSECT INTERACTIONS, PHENOLOGY, AND BREEDING SYSTEM

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ABSTRACT

Lomatium bradshawii (Bradshaw's lomatium) is a state and federally listed endangered species that occurs in fragmented native-prairie habitat in western Oregon and southwestern Washington. A U.S. Fish and Wildlife Service recovery plan for the species identifies breeding-system and pollinator-availability research as needed for filling information gaps that could influence recovery efforts. We conducted field experiments and observations to document the importance of these issues to the species' conservation. A pollinator exclusion experiment showed that insects are required for fruit production in *L. bradshawii*. Because the species does not reproduce vegetatively or maintain a persistent soil seed bank, reduction or elimination of insect pollinators through destruction of nesting habitat or application of insecticides in or adjacent to critical habitat could result in rapid population decline. A large diversity of insects, including at least 38 species of bees, flies, wasps, beetles, and others visited *L. bradshawii* flowers throughout the species' range, so it is unlikely that the management and recovery of the species is vulnerable to failure due to population fluctuations of any one insect taxon. Insects are required for pollination because *L. bradshawii* has a complex breeding system (protogyny) that inhibits self-fertilization through a temporal separation of the sexual phases of flowers within an inflorescence. Also, the first umbel displayed on a given plant is generally all-male (with no fruit-producing flowers), while the second umbel produces an average of twenty-four hermaphroditic flowers. We hypothesize that *L. bradshawii* populations have high genetic diversity because of the apparently high outcrossing rate, especially in the west Eugene area where the existing patches may represent fragments of formerly larger and interconnected populations. Also, we recommend that habitat protection and management for *L. bradshawii* take into account nesting habitat for pollinating insects.

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INTRODUCTION

Lomatium bradshawii (Bradshaw's lomatium) is listed by the U.S. Fish and Wildlife Service (USFWS), the Oregon Department of Agriculture (ODA), and the Oregon Natural Heritage Program (ONHP) as an endangered species (ONHP, 1993). The conservation of the species is therefore of mutual concern to federal, state, and other agencies. Because of this common interest, the Oregon Department of Agriculture and the BLM Eugene District have entered into a cooperative project to conduct applied research into the biology of the species. Tools and background information for management of the species and its habitat are needed to ensure long-term population sustainability in a fragmented landscape. A Recovery Plan for *L. bradshawii* (Parenti *et al.*, 1993) targets examination of pollinator availability, impacts of insects, and inbreeding depression as priority tasks (among others) needed to meet recovery objectives for the species. The goal of this report is to present information on these aspects of the biology of *L. bradshawii*, including continued research into the breeding system of the species, identity and distribution of insect pollinators (expanded from past studies to include populations on BLM land and other sites), and the importance of these insects for pollination and seed production.

Lomatium bradshawii (Figure 1) is a member of the Apiaceae, the parsley family. Individual plants are not able to send out runners or develop rhizomes for vegetative spread. Instead, *L. bradshawii* is a taprooted perennial that reproduces by seed only. The species is known from several fragmented populations in the Willamette Valley of western Oregon and one from southwestern Washington. Its habitat is wet prairie and oak savannah, either on deep clay soils dominated by *Deschampsia cespitosa* (tufted hairgrass) of valley bottoms, or thin soils saturated in spring over foothills-basalt (Parenti *et al.*, 1993; see Kaye *et al.* 1994, for more details on the species' habitat).

Plant species that rely on insects for pollination are vulnerable to the loss of their pollinators, for without them, they are unable to produce seeds and new individuals. The Willamette Valley is an intensely managed and farmed area. Every year a huge acreage, including fields, fence rows, and roadsides, is sprayed with insecticides and herbicides. Local destruction of pollinating insects and their nesting habitat is cause for concern, especially when the full ecological role of these insects is unknown. Insecticide applications, such as aerial spraying of fenitrothion, can reduce bumblebee populations (Plowright *et al.* 1978, Plowright and Rodd 1980), which in turn may be responsible for observed declines in fruit and seed production of common plants (Thaler and Plowright 1980, Hanson and Osgood 1984). Currently, we have no assessment of the risk of pollinator loss to the survival and recovery of *L. bradshawii*, and it is unknown whether the species can produce seeds in the absence of pollinating insects (Kaye 1992). Very few studies

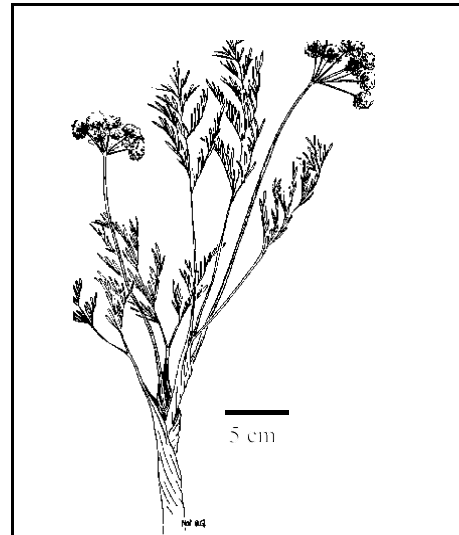


Figure 1. *Lomatium bradshawii* is an endangered species of Willamette Valley prairies. Drawing from Meinke (1981).

have been published that document the breeding system and pollination biology of members of the Apiaceae (but see Bell 1971; Lindsey 1982, 1984; Lindsey and Bell 1985) and fewer still have described the situation for species of *Lomatium* (Hardin 1929, Schlessman 1978). Some observations of floral visitors to *L. bradshawii* and of the species' inflorescence structure are available, but these observations are either of limited geographic scope or are qualitative only (Kaye 1992). Therefore, more detailed work is needed to document the floral biology, and identity and role of insect pollinators of *L. bradshawii*.

Objectives--The objectives of this research are to:

- Determine if *Lomatium bradshawii* is capable of setting seed in the absence of pollinating insects.
- Evaluate the breeding system and floral phenology of *L. bradshawii*.
- Determine the identity and distribution of pollinating insects at *L. bradshawii* populations in the Willamette Valley, Oregon.

METHODS

Study sites--The following observations and experiments were conducted at one or more of the following sites in the Willamette Valley, Oregon (Figure 2): (1) Fisher Butte Research Natural Area (RNA), Army Corps of Engineers property west of Eugene, Lane County; (2) Buford County Park, east of Eugene, Lane County; (3) Short Mountain Land Fill southeast of Eugene, Lane County; (4) Long Tom Area of Critical Environmental Concern (ACEC), BLM property northwest of Eugene, Lane County; (5) Finley National Wildlife Refuge (NWR), USFWS property south of Corvallis, Benton County; and (6) Jackson-Frazier wetland north of Corvallis, Benton County. *Lomatium bradshawii* populations at these sites are described in more detail in Parenti *et al.* (1993).

Pollinator exclusion--To determine if *Lomatium bradshawii* requires insects for cross-pollination and fruit-set, we conducted a pollinator exclusion experiment at the population at Fern Ridge Reservoir in the Fisher Butte RNA (1). Sixteen pairs of plants (each with two umbels) were arbitrarily selected from a relatively uniform area of habitat, and one plant from each pair was selected at random for exclusion of pollinators. Pollinator exclusion cages were established on April 16, 1993, while the second umbel was still immature, to prevent insect visits to the flowers when they opened. The 16 remaining plants were tagged but not covered. On May 21, 1993, we re-visited the caged plants to verify that the enclosures had not been disturbed, and inspect the plants within to confirm that development of inflorescences was not hindered by the presence of the cage. On June 8, 1993, the number of fruits produced on both caged and uncaged plants was recorded. We used a Wilcoxon signed-rank test to test for a significant ($\alpha \leq 0.05$) effect of caging (lack of pollinating insects) on fruit set.

Phenology and umbel structure--We examined umbels from plants at the Fisher Butte population to quantify differences in sexual expression between one-umbel plants and two-umbel plants. Ten plants of each type (one- and two-umbel) were selected at random from throughout the *Lomatium bradshawii* population. All umbels were removed from these plants on April 27, 1993, placed in separate plastic bags, and examined under a dissecting microscope within two days of collection. We kept track of whether an umbel was displayed first or second to examine the effect of emergence sequence on hermaphroditic flower production in two-umbel plants. Sexual expression was evaluated by recording the number of umbellets per umbel, the number of flowers per umbellet, and the number of hermaphroditic flowers per umbellet to determine total flower production and the relative abundance of hermaphroditic flowers on umbellets in different positions. Hermaphroditic flowers possessed ovaries that were swollen and large (≥ 1 -mm), making them easy to distinguish from male flowers, which lacked swollen ovaries. We used a Mann-Whitney U-test to compare ($\alpha \leq 0.05$) single umbels with first umbels, and first umbels with second.

Insect visitors--We visited six populations on one or more days in 1990, 1991, and 1993 to observe and collect insect visitors for identification and examination of pollen load. These populations included Buford Park, Amazon Park, Finley NWR, and Jackson-Frazier Wetland, discussed by Kaye in an earlier publication (1992), and two additional sites, Long Tom ACEC and Short Mountain Land Fill, not previously examined for insects. Insects were collected with a net, killed in an acetone killing jar, and inspected for pollen under a dissecting microscope. Although *Lomatium bradshawii* pollen is characteristically yellow and easily distinguished from pollen of different colors, the identity of yellow pollen on insect bodies was not confirmed.

Figure 2. Study sites for *Lomatium bradshawii* pollination research in the Willamette Valley, Oregon.

RESULTS

Pollinator exclusion--Our caging experiment at Fisher Butte RNA indicated that *Lomatium bradshawii* does not self-pollinate (Figure 3). Second umbels on caged plants rarely formed any fruits (mean=0.13 per umbel, SE 0.08), while those available to pollinating insects produced an average of 10.8 fruits (SE 1.85). This difference was highly significant ($P<0.0001$).

Phenology and umbel structure--Umbel sequence and umbellet position had a significant ($P=0.00011$) effect on the production and distribution of hermaphroditic flowers on two-umbel plants. However, the number of flowers per umbellet was not significantly effected by umbel sequence. On average, second umbels had significantly ($P=0.00011$) more hermaphroditic flowers (24.4 ± 5.35) than first umbels (1.0 ± 0.67). In addition, these flowers were encountered only on outer umbellets; inner umbellets produced staminate flowers only (Table 1, Figure 3), observations which are consistent with previous qualitative descriptions of *Lomatium bradshawii* (Kagan 1980, Kaye 1992). One of the outer umbellets developed faster than the others, causing it to be extended beyond the rest of the umbel. This umbellet is here termed the 'lead umbellet' (Figure 3). Approximately half of all hermaphroditic flowers produced on an umbel were carried by the lead umbellet, and the lead umbellet on a second umbel produced significantly ($P=0.0001$) more hermaphroditic flowers (13.7 ± 1.14) than on a first umbel (0.5 ± 0.5). Put another way, hermaphroditic flowers out-numbered staminate flowers more than two to one on a lead umbellet from a second umbel, but on a first umbel the lead umbellet was dominated by staminate flowers by a margin of thirty-three to one (Table 1).

The first umbel on two-umbel plants was similar in most respects to the single umbel on one-umbel plants, with the exception that first umbels had slightly but significantly ($P=0.02$) more umbellets than single umbels (Table 1). Therefore, plants that produce only one umbel in a given season are rarely capable of producing any seeds, and contribute only pollen as their reproductive effort.

Insect visitors--A large diversity of insects were observed visiting flowers of *Lomatium bradshawii* from 1990 to 1993. In all, we collected 185 insect specimens in at least 38 species

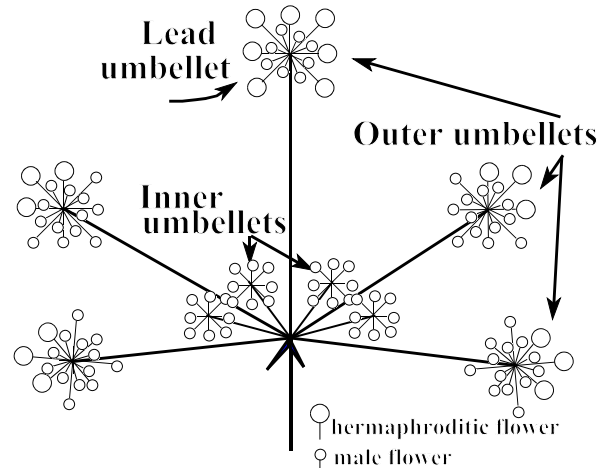


Figure 3. Typical umbel structure of *Lomatium bradshawii*. Outer umbellets may bear hermaphroditic flowers (and therefore may produce fruits), while inner umbellets produce male flowers only. The lead umbellet is the largest and first to emerge, and generally displays the largest number of hermaphroditic flowers. Modified after Lindsey (1982).

from seven *L. bradshawii* populations. The majority of these insects were solitary bees (7 spp.), syrphid flies (11 spp.), and other flies (10 spp.), but a smaller number of wasps (2 spp.), caddisflies (1 spp.), planthoppers (1 spp.), true bugs (1 spp.), beetles (4 spp.), and ants (1 spp.) were also collected (Table 2). No single insect species dominated the pollinator fauna. Most taxa were restricted to one or two *L. bradshawii* populations, but a few bees, flies, and one beetle were collected from four or five sites. Two very small fly species did not carry pollen and were unlikely pollinators. Also, ants observed on umbels at the Jackson-Frazier (J-F) population did not carry pollen, seldom moved among plants and were probably ineffective pollinators. However, twenty-six species, mostly bees and syrphids, carried pollen on their bodies or legs (Table 2), demonstrating their potential ability to cross-pollinate *L. bradshawii*, and most insects frequently moved from one plant to another. The relative abundance of bees, flies, and other insects (as measured by number of specimens collected) differed from site to site and year to year. For example, bees only were observed at Finley NWR in 1990, but in 1991 no bees were observed and flies represented 83% of the collections. And although flies dominated most sites in 1993, only bees were observed at Short Mountain that year. These spatial and temporal differences may be related to weather conditions, chance, or other factors.

Table 1. Flower production and sexual expression within *Lomatium bradshawii* umbels and umbellets. Mean (SE) values are from ten samples each of single umbels from one-umbel plants and the first and second umbels from two-umbel plants. All samples were taken from Fisher Butte RNA. Hermaphroditic flowers are denoted $\sigma\text{♀}$, and staminate flowers are indicated as σ . Asterisks by first-umbel values indicate a significant difference from single-umbel means. Asterisks by second-umbel values indicate a significant difference from first-umbel means.

	ONE-UMBEL PLANT		TWO-UMBEL PLANT	
	Single umbel	First umbel	Second umbel	
<i>umbellets/umbel</i>	6.2 (0.63)	8.6 (0.73)*	9.2 (0.63)	
<i>$\sigma\text{♀}$ flowers/umbel</i>				
lead	0.1 (0.1)	0.5 (0.5)	13.7 (1.14)***	
outer	0.1 (0.1)	1.0 (0.67)	24.4 (5.35)***	
inner	0.0	0.0	0.0	
all umbellets	0.1 (0.1)	1.0 (0.67)	24.4 (5.35)***	
<i>flowers/umbellet</i>				
lead	16.6 (1.95)	18.6 (2.19)	21.1 (1.17)	
outer	8.1 (0.74)	9.8 (0.83)	9.5 (0.55)	
inner	5.3 (0.63)	6.9 (0.92)	6.5 (0.60)	
all umbellets	7.12 (0.5)	8.4 (0.80)	8.0 (0.46)	
<i>ratio: $\sigma\text{♀}/\sigma$</i>				
lead	0.005 (0.005)	0.03 (0.03)	2.1 (0.33)***	
outer	0.001 (0.001)	0.01 (0.009)	0.7 (0.16)***	

inner	0.0	0.0	0.0
all umbellets	0.0006 (0.0006)	0.009 (0.007)	0.4 (0.09)***

* $P < 0.05$; *** $P < 0.0001$

Table 2. Insect visitors to *Lomatium bradshawii* flowers at six sites in the Willamette Valley, 1990-1993. Numbers indicate how many specimens of each taxon were collected. Only the family name is given when the genus is unknown.

	Buford 1990	Buford 1991	Buford 1993	Finley 1990	Finley 1991	Finley 1993	J-F 1991	J-F 1993	Amazon 1991	LT 1993	Short 1993	Misher 1993
Solitary bees												
<i>Andrena</i> sp. 1†		7		3								
<i>Andrena</i> sp. 2†		1										
<i>Andrena</i> sp. 3†				4			3				1	1
<i>Ceratina</i> sp.†					5							4
Halictidae sp. 1†			1				1				1	
Halictidae sp. 2†									1			
<i>Lasioglossum</i> sp.†					1		1	1			2	1
Syrphid flies												
<i>Cheilosia</i> sp.			1									
<i>Melanostoma</i> sp.†						1						
<i>Mesograpta marginata</i> †			1					1				
5												
<i>Paragus</i> sp.†								18	1		1	1
<i>Platycheirus</i> sp.†							1					
<i>Rhagio</i> sp.†									7	1		
<i>Sphaerophoria</i> sp. 1†								5	1			
<i>Sphaerophoria</i> sp. 2†							1					7
<i>Syrphus</i> sp.†				3								
<i>Toxomerus</i> sp.†							1					
<i>Xylota</i> sp.†	1		2									
Other flies												
Anthomyiidae sp. 1†			1	4		5	1	1				
Anthomyiidae sp. 2†							5				9	
Calophoridae sp.	1											
Empididae sp. 1			3					5		6		
Empididae sp. 2**						3						
Empididae sp. 3†							1					

DISCUSSION

Importance of insects for pollination--Insect pollinators are required for fruit production in *Lomatium bradshawii*. Therefore, the maintenance of populations and recovery of the species relies on healthy insect pollinator abundances because *L. bradshawii* does not reproduce vegetatively. Furthermore, the species does not maintain a persistent soil seed bank (Kaye *et al.*, 1994), so pollinator loss could result in immediate population decline. In the long run, protecting the nesting sites of insect pollinators may be a necessary component of conservation efforts for *L. bradshawii*. A three-mile radius no-spray zone around endangered plant populations (Tepedino 1990) may be excessive to protect pollinators of *L. bradshawii* from insecticide applications, but some measure of habitat protection beyond the immediate site occupied by the rare plants should be considered. Habitat protection for beneficial insects should include prohibition of insecticides and protection of nesting areas from physical disturbance.

Umbel structure, phenology, and sexual expression--Although some self-pollination may occur in *Lomatium bradshawii*, the probability of cross pollination is increased because staminate and hermaphroditic flowers within a single inflorescence mature at different times. This type of breeding system may be the result of natural selection for out-crossing, and thus gene flow, to offset the deleterious effects of inbreeding (Lloyd and Webb 1986). Past efforts by Kagan (1980) and Kaye (1992) to test for self-pollination in *L. bradshawii* failed for various reasons, but it is now clear that the species does not self-pollinate. This is in contrast to a second rare species of *Lomatium*, *L. greenmanii* of the Willowa Mountains in northeastern Oregon, which sets abundant fruit even when caged to exclude pollinating insects (Kaye, 1993). Other genera in the Apiaceae, such as *Thaspium* and *Zizia*, are typically self-compatible but rarely self-pollinate because of a strong out-crossing system resulting from dichogamy and floral phenology. This system is also present in *L. bradshawii*, as described below.

Description of *Lomatium bradshawii* breeding system and floral phenology

Lomatium bradshawii is andromonoecious, each plant bearing hermaphroditic (with functional male and female parts) and staminate (male parts only) flowers. The staminate flowers do not have functional ovaries and therefore do not set seed. Hermaphroditic flowers are protogynous: the styles elongate and display the stigmatic surfaces prior to anther dehiscence and pollen release. Reproductive plants produce one or two (rarely three or more) compound umbels, borne singly atop scapose (leafless) peduncles.

The first umbel to emerge on a given *Lomatium bradshawii* is almost exclusively composed of staminate flowers, while later umbels have a higher proportion of hermaphroditic flowers (33% hermaphroditic flowers on second umbels), a pattern observed in previous studies of *L. bradshawii* (Kagan 1980, Kaye 1992), *L. farinosum* (Schlessman 1978) and other Apioid genera, such as *Zizia* and *Thaspium* (Lindsey 1982, Lindsey and Bell 1985). Thompson (1984) observed that in *Lomatium grayi*, about 70% of the plants that produced hermaphroditic flowers first produced one or more all-male umbels before producing any umbels with hermaphroditic flowers.

Within an umbel, *Lomatium bradshawii* umbellets develop sequentially. The outer series of umbellets matures before the inner series, and the outer flowers of the outer umbellets develop before the inner flowers, resulting in protogyny within umbels and umbellets. In addition, the hermaphroditic flowers are more common on the outer umbellets, and more common on the *outer edge* of the outer umbellets (Figure 3). One of the outer umbellets develops faster than the others, causing it to be extended beyond the rest of the umbellets. This umbellet is here termed the 'lead umbellet' and differs from the others in having more hermaphroditic flowers (Figure 3); we hypothesize that this lead umbellet serves to separate temporally the reproductive functions of outer umbellets within the umbel. Lead umbellets are not discussed in previous descriptions of *Lomatium* or other Apiaceae genera.

Dichogamy in *Lomatium bradshawii* is expressed as protogyny within umbels (stigmatic surfaces are receptive first) and by protandry on a whole-plant basis (the first umbel is male). This combination of dichogamous mechanisms may represent a compromise between protogyny and androgyny for restricting self-fertilization, optimizing pollen release and reception, and avoidance of pollen-stigma interference (Lloyd and Webb, 1986).

Insect visitors--Floral visitors to *Lomatium bradshawii* are diverse and appear widely capable of pollinating the flowers. No single insect species dominated the pollinator fauna in three years of observations. Because of this diversity, *L. bradshawii* range-wide may not be vulnerable to population swings of any one insect species. At least 38 insect species were observed visiting inflorescences of *L. bradshawii*, up from past observations of 25 possible pollinators (Kaye 1992). Although *L. bradshawii* blooms early in the spring (usually beginning in April) before many insect species are active, a large variety of bees, flies, and other insect taxa have been collected. Solitary bees, many of which are specialists, are well known as important pollinators of many plants in habits ranging from the Arctic (Armbruster and Guinn 1989) to temperate regions (Frankie *et al.* 1976, Strickler 1979, Motten 1986). One bee that we observed visiting *L. bradshawii*, *Andrena* sp., may be the same species observed by Kagan (1980) at Long Tom ACEC and Willow Creek (The Nature Conservancy Preserve west of Eugene). The solitary bees we observed were all capable of carrying pollen on their legs and/or bodies, and appeared to be effective pollinators.

The presence of flies as potential pollinators is somewhat unexpected. Muscoid flies, especially, are not well known as pollinators at low elevations, although they have been observed as casual or important pollinators in montane and alpine areas such as the Washington Cascades (Shaw and Taylor 1986), Rocky Mountains (Kearns 1990), Adirondacks (Levesque and Burger 1982), and Chilean Andes (Arroyo *et al.* 1982) on a variety of plant taxa. Syrphid flies are more often reported as pollinators or floral visitors than muscoid flies, and they are known from a very wide range of habitats and elevations. Despite inefficient pollen transfer, muscoid and syrphid flies may be important pollinators because they are active during cold or wet weather (Levesque and Burger 1982); they are often present during inclement weather in early spring at *Lomatium bradshawii* sites. Lindsey (1984) documented syrphid importance for pollination of *Zizia* at one examined site, and weather conditions best explain diel (daily) patterns of all insects on *Tilia* and

Heracleum (Wilmer 1983) .

Although umbels have a reputation as being "promiscuous" (Grant 1949) because of their non-specialized inflorescences from which many types of insects can successfully harvest resources, they may be subtly capable of inducing constancy and efficiency in some insects. For example, despite a large number and great diversity of insect visitors to *Zizia* and *Thaspium* (Apiaceae), only one to four insect species account for at least 74% of pollination at all sites surveyed (Lindsey 1984). Cryptic variation in floral and inflorescence characters in these genera enhances specialization for pollination by syrphid flies and solitary bees (Lindsey and Bell 1985). As with solitary bees, some syrphid fly species are more constant foragers than others, as revealed by analyses of gut contents (Haslett 1989) and pollen load (Lindsey 1984: Apiaceae; Leereveld *et al.* 1981: *Scirpus maritimus*), and field behavior in alpine systems (Levesque and Burger 1982, Shaw and Taylor 1986). The relative constancy and pollination effectiveness of the bees and flies that visit *L. bradshawii* is currently unknown, but the attractiveness of *L. bradshawii* to a diversity of insect visitors may result in successful pollination under various climatic conditions. Indeed, the differences in insect abundance from site to site and year to year observed in this study may, in part, result from differences in weather conditions during observation periods (Kaye 1992). Also, pollination by diverse insect taxa may improve pollination success by simply increasing the number of available pollinators or through some positive interaction. For example, honey bees and house flies are better pollinators of carrots (*Daucus carota*: Apiaceae) in combination than alone (Wilson, *et al.* 1991).

Summary--Insect pollinators are crucial for fruit production in *Lomatium bradshawii*. Because the species does not reproduce vegetatively or maintain a persistent soil seed bank, reduction or elimination of insect pollinators through application of pesticides could result in rapid population decline. A large diversity of insects visit *L. bradshawii* flowers throughout the species' range, so it is unlikely that the management and recovery of the species is vulnerable to failure due to population fluctuations of any one insect taxon. The complex breeding system and floral phenology of *L. bradshawii* apparently block self-fertilization, resulting in a complete dependence on insects for pollination and genetic exchange. We hypothesize that *L. bradshawii* populations have high genetic diversity because of the apparently high outcrossing rate, especially in the west Eugene area where the existing patches may represent fragments of formerly larger and interconnected populations. Also, we recommend that habitat protection and management for *L. bradshawii* take into account nesting habitat for pollinating insects.

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